



1986 Redux: New genera of anoles (Squamata: Dactyloidae) are unwarranted

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Introduction

The year 1986 gave us Madonna's *True Blue*, Geraldo Rivera opening Al Capone's vaults, and a new taxonomy of anoles (Guyer and Savage, 1986). Each of these greatly anticipated events began with considerable promise but ended up adding nothing of depth to the culture of the time. Madonna's best work was behind her, Capone's vaults were a letdown, and the proposed anole taxonomy was unsupported and poorly executed (Cannatella and de Queiroz, 1989; Williams, 1989), but was mostly done in by the paucity of data available at the time. In the ensuing years, Madonna showed some staying power and Geraldo reinvented himself, but the erection of a handful of nonmonophyletic genera was not enough to achieve the apparent goal of preserving Savage's (1973) genus *Norops* as a valid name for anole lizards with transverse processes on their posterior caudal vertebrae (Etheridge, 1959). The genera *Dactyloa*, *Ctenonotus*, *et al.* lived on in Savage's (2002) excellent Costa Rica guide but were mostly ignored by those not working in Costa Rica.

In 2012 we have Lady Gaga continuing Madonna's tramp-diva legacy, TMZ filling Geraldo's gossip-news niche, and an ostensibly new taxonomy of anoles from Nicholson *et al.* (2012). But just as Lady Gaga recycles Madonna and TMZ unnecessarily claims Geraldo's old job, the anole taxonomy of 2012 doesn't offer much that is new, and doesn't improve much on something that was misguided and unfortunate in 1986. Below I argue why it would be scientifically irresponsible to adopt the Nicholson *et al.* (2012) taxonomy for anoles. Nicholson *et al.* (2012) selectively adopted results of their own flawed, unstable, and conflicting analyses, selectively incorporated pertinent published data and results, and changed names for over 100 species that have never been included in a phylogenetic analysis. The proposed taxonomy is unnecessary and unwarranted according to standard taxonomic practice. It should not be adopted by the scientific or nonacademic communities.

Below I focus on taxonomic issues. Other problems with Nicholson *et al.* (2012) will be addressed elsewhere. I use 'Nicholson *et al.*' to refer to the 2012 paper, and list species names without generic designations.

Some of the proposed genera are not monophyletic

Although debates over Linnaean versus phylogenetic taxonomy continue, pretty much every working systematist today agrees that genera, if they are to be recognized, must be monophyletic. Remarkably for a published taxonomic paper, most of the genera proposed by Nicholson *et al.* do not meet this minimum requirement. This fact is a major problem with their taxonomy--the proposed genera are demonstrably not valid according to nearly universally accepted standards of animal taxonomy. Table 1 summarizes this conclusion with reference to the two trees evaluated by Nicholson *et al.* and an additional tree published a year earlier (Alfoldi *et al.*, 2011) that included much more character data than Nicholson *et al.* The analysis that includes the most characters (Alfoldi *et al.*, 2011) recovers two of the proposed genera as nonmonophyletic, and the analysis that includes the most taxa—Nicholson *et al.*'s Fig. 5—recovers five of the proposed genera as nonmonophyletic. The species groups continue the theme of taxonomic assignment that only partially follows their phylogenetic results. Of the 23 species groups of Nicholson *et al.* that are not monotypic, six are not monophyletic in their most densely sampled tree.

Even if one were to ignore 'problematic' taxa in order to preserve the monophyly of the proposed genera (which I do not advocate doing), the remaining genera are extremely poorly supported. For example, suppose we exclude *occultus*, *darlingtoni*, *argenteolous*, *lucius*, *bonairensis*, *chloris*, *peraccae*, *apollinaris*, *christophe*, and *barbouri* in order to render the proposed genera monophyletic in the tree of Nicholson *et al.* that includes the most taxa and data (Nicholson *et al.*: Fig. 5). In this case, seven of eight genera are supported at bootstrap values of less than 50%.

TABLE 1. Assessments of monophyly for the Nicholson *et al.* (2012) genera.

Genus	Nicholson <i>et al.</i> Combined 240 sp; 1580 chars	Nicholson <i>et al.</i> Molecular 189 sp; 1482 chars	Alfoldi <i>et al.</i> 93 sp; 20000 chars
<i>Norops</i>	Monophyletic	Monophyletic	Monophyletic
<i>Dactyloa</i>	Nonmonophyletic	Monophyletic	Monophyletic
<i>Audantia</i>	Monophyletic	Monophyletic	Monophyletic
<i>Deiroptyx</i>	Nonmonophyletic	Monophyletic	Monophyletic
<i>Chamaelinorops</i>	Nonmonophyletic	Nonmonophyletic	Nonmonophyletic
<i>Xiphosurus</i>	Nonmonophyletic	Nonmonophyletic	Nonmonophyletic
<i>Ctenonotus</i>	Monophyletic	Monophyletic	Monophyletic
<i>Anolis</i>	Nonmonophyletic	Nonmonophyletic	Monophyletic

These monophyly issues indicate that Nicholson *et al.* were inconsistent in their criteria for assigning species to named groups. In many cases they used a criterion of monophyly with reference to their presented trees, but in some cases they ignored their results. That is, they must have either speculated that their named genera and species groups will eventually be monophyletic when additional data are analyzed or, like some precladistic authors (e.g., Mayr, 1969), they employed some criteria for generic membership in addition to monophyly. For example, neither of their presented trees groups *christophei* with other members of their *Chamaelinorops*, yet they assigned *christophei* to the genus *Chamaelinorops*. And *chloris* and *peraccae* group with non-*Dactyloa* in the only tree where those taxa appear (their Fig. 5), yet for some reason Nicholson *et al.* consider these taxa to be part of *Dactyloa*. In some cases they ignored their combined results and accepted their molecular results (e.g., *occultus*), whereas in others they ignored their molecular results in favor of the combined tree (e.g., *lucius*). Certainly monophyly is their main criterion for generic membership, and they did attempt to explain some of their exceptions to this criterion. But many exceptions were not explained, and it is difficult to discern a consistent pattern among the exceptions. Regardless of their intentions, their subjective decisions are indicative of the flimsy support for their genera.

Not enough taxa, not enough characters

Nicholson *et al.* claim a "stable" taxonomy for 95% of anole taxa. This 95% figure is hard to believe when 147 currently recognized species of *Anolis* (38% of the genus if we accept Nicholson *et al.*'s estimate of 387 species of *Anolis*) were not included in their phylogenetic analyses. Most of these 147 species were assigned new generic names by Nicholson *et al.* even though they have not been scored for characters that might allow their phylogenetic placement.

But even when excluded species eventually are scored for the supposedly diagnostic characters listed by Nicholson *et al.*, the diagnoses will be of no help in placing such species, for two reasons. First, most of the diagnoses are for genera that are not monophyletic (Table 1). For example, the diagnosis of *Dactyloa* was not estimated including all analyzed members of the proposed group because the clade for which diagnostic apomorphies are listed excludes purported *Dactyloa* members *chloris*, *peraccae*, and *apollinaris* (see Nicholson *et al.*: Fig. 5). If these species were constrained to occur within the *Dactyloa* clade, the diagnosis is likely to change. Second, the diagnoses are based on a single tree from a sample of 4999 equally optimal trees. If any other tree had been chosen from this sample, the diagnoses would be different. This fact completely undermines their diagnoses. There is no point in listing detailed clade support for a single tree when there exists an additional 4998 trees that are equally well supported.

The group definitions are equally unhelpful. Almost all of these are based on limited information. That is, conditions for most traits have not been published for most species. For example, morphological states for most defining characters for 52 of 83 *Dactyloa* species have not been published. In some cases, groups are defined based on incorrect information. For example, the listed definition of the *distichus* species group states that these species possess "middorsal scales on snout not in a regular pattern," even though all species in this group possess middorsal snout scales in a regular parallel pattern (Poe, 2004; this trait is the source of the name 'distichus'). In many cases, the traits listed in a definition are uninformative. For example, *Dactyloa* is defined as displaying "angular process of articular may be large or reduced or absent." That is, all conditions of the angular process—large, reduced, absent—are observed in this clade. This being the case, why mention the trait at all? I am unable to discern how Nicholson *et al.* arrived at their group definitions; each seems to constitute a haphazard sample of traits, some of which apply to some members of the defined group.

The general problem is the same one that was present in 1986. That is, there are not enough data to reclassify all the anoles. More than a third of the genus has not been analyzed phylogenetically. Many taxa that have been analyzed are scored for so few characters that their phylogenetic placement is unreliable. The one relatively large data set that is available (the mitochondrial segment of 1400+ characters) is unable to resolve deep relationships strongly (Jackman *et al.*, 1999). This paucity of data leads to poorly supported nodes in the presented trees and thus poorly supported genera of Nicholson *et al.* Only one of the eight proposed genera is both monophyletic and supported at greater than a 50% bootstrap level (Nicholson *et al.*: Fig. 5). Perhaps more extensive character sampling and the addition of the remaining 100+ species of anoles will produce groups compatible with the Nicholson *et al.* generic designations—certainly this result seems likely for *Norops*, *Audantia*, and perhaps *Dactyloa*, as these groups frequently have been recovered as monophyletic (Etheridge, 1959; Poe, 2004; Jackman *et al.* 1999; Nicholson, 2002; Castañeda and de Queiroz, 2011; Alföldi *et al.*, 2011). But for most of their genera there seems no reason to think that the addition of characters and taxa will fortuitously turn named groups into clades.

The situation could have been improved slightly by the inclusion of all data that were available to the authors. Nicholson *et al.* omitted lots of published data from their analyses. For example, they failed to include over 20000 sites of DNA sequence data from Alföldi *et al.* (2011) which were scored for many of their included taxa. And they excluded several taxa scored for over 4000 sites of DNA sequence data by Castañeda and de Queiroz (2011). Both of these papers were available to the authors--Nicholson *et al.* pointed out cases where results of these papers supported their conclusions. It is not clear why these data were excluded from their analyses.

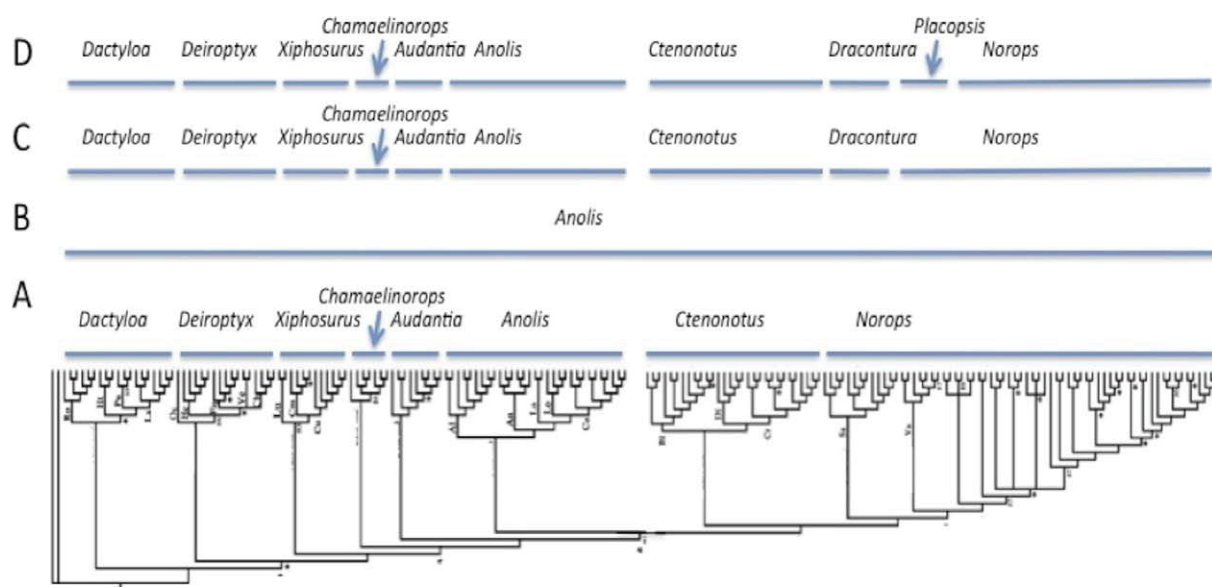


FIGURE 1. Alternative valid generic designations among anoles, assuming the molecular tree of Nicholson *et al.* (2012: Fig. 4).

The future of anoline genera

The above arguments detail why it would be scientifically irresponsible to recognize the genera proposed by Nicholson *et al.* The results of the analyses are not compatible with recognition of the proposed genera. Just as in 1986, there is no way to maintain recognition of *Norops*—which everyone agrees is monophyletic—as a genus without erecting questionably monophyletic or outright nonmonophyletic genera. The same arguments that applied to the initial Guyer and Savage (1986) foray apply to Nicholson *et al.* 26 years later.

But at some point, it is hoped in the near future, we will have a set of strongly supported clades within *Anolis*. At that point, should we divide *Anolis* up into multiple genera? Below I question the rationale for arguing for eight genera versus one (as in Nicholson *et al.*), or for more or fewer than eight genera.

For the sake of argument, let us accept the molecular tree of Nicholson *et al.* (Fig. 4) because this tree is most compatible with their genera. The generic rearrangement of Nicholson *et al.* is shown in fig. 1A. In this case, the generic assignments of Nicholson *et al.* are mostly in agreement with accepted practices of taxonomy (ignoring exceptions such as *christophei*). Let's call this taxonomic scheme the "Preserve *Norops* " (PN) scheme. The rub, of course, is that an arrangement that calls the entire clade *Anolis* (fig. 1B) also is scientifically valid. Let's call this scheme, of regarding all anoles as *Anolis*, the "Keep *Anolis* Whole" (KAW) approach. Systematists agree that genera must be monophyletic in order to be scientifically valid, and both these schemes name groups based on monophyly.

The KAW approach is valid and PN is valid if we fudge things, given the subset of data that we have adopted in our example. In this case, Nicholson *et al.* argue that we should recognize PN because recognition of a single genus *Anolis* "underemphasizes the evolutionary diversity within the family and obfuscates major biological differences among clades." But if more genera is better—if eight is better than one—why not recognize nine genera instead of eight? Figure 1C shows an arrangement that is scientifically valid, i.e., completely compatible with the phylogenetic results, but includes nine genera. Why not adopt this taxonomy? But then, figure 1D shows a scheme with 10 genera, including separate generic names for Cuban, Jamaican, and mainland Beta *Anolis* (i.e., *Norops* is divided into three genera). This arrangement makes a lot of biogeographic sense, and also is scientifically valid, so why not recognize these 10 genera rather than the Nicholson *et al.* scheme? One can see that following this argument to its logical conclusion ends in assigning a separate genus for each species, i.e., in uninformative absurdity. At the other end of this line of logic, in the KAW realm, the similarity of all anoles is emphasized over Nicholson *et al.*'s view of difference and the entire group is called *Anolis*. The problem that should be obvious is that there is no good scientific reason for choosing among these options. The PN and KAW arrangements, along with any other scheme where clades are assigned generic names, are equally valid under current conventions of taxonomy. The phylogenetic results of Nicholson *et al.* do not require their proposed changes in taxonomy. Their results do not require any changes in taxonomy at all.

Thus, even once we finally have a well-resolved and strongly supported estimate of anole phylogeny, there will be no *scientific* reason to prefer a taxonomy like Nicholson *et al.*'s that preserves *Norops* over any other taxonomy such as KAW that also recognizes monophyletic groups. Arguments about the number of genera to recognize then turn on human perceptions like Nicholson *et al.*'s "major biological differences" rather than anything inherent to the natural world. If evaluated as arguments based on objective evidence, these are bound to fail. Anyone who has tried to distinguish females of "*Audantia*" *cybotes*, "*Norops*" *sagrei*, and "*Ctenonotus*" *crisatellus* in southern Florida is likely to question how "major" the supposed "biological differences" are between these genera. A biogeographer's major biological differences may not resemble those of a comparative anatomist or a geneticist, and arguing which set of differences more warrants generic designation is pointless. The arguments of Nicholson *et al.* for recognizing eight genera over one are not based on nature and thus give no scientific justification for their taxonomy.

Given that there eventually will be no scientific reason for choosing between KAW and something like PN, what should we do? Adoption of PN would require researchers and interested nonacademic people to learn a suite of unfamiliar names for familiar lizards, and would necessitate changing large databases as well as labels for thousands of jars of museum specimens. Switching to PN from KAW would create confusion over the longstanding use of the name *Anolis* in research, and would fracture the taxonomic connection linking the huge body of research on *Anolis*. Alternatively, we can continue to recognize a single genus *Anolis* and experience none of these downsides. Well-supported clades within *Anolis* such as *Norops* may be named based on the principles of phylogenetic taxonomy (de Queiroz and Gauthier, 1992). This latter approach is conservative in that it follows entrenched practices (*Anolis* remains more familiar than the Nicholson *et al.* genera) and stable in that it is highly unlikely that *Anolis* will turn out to be nonmonophyletic (unlike the Nicholson *et al.* genera, most of which currently are nonmonophyletic; Table 1). Furthermore, it allows for uncertain taxa to be assigned to genus and also to other clades that we can be sure they belong rather than requiring that all taxa be pigeonholed into poorly supported, taxonomically equivalent genera.

These reasons for preferring a single genus *Anolis*—stability, entrenchment, and a satisfying way to deal with uncertain taxa—are not scientific reasons for preferring this scheme; they are sociological and practical arguments. But then, there are no scientific arguments for recognizing genera beyond arguments about monophyly, and a PN scheme may someday be built around monophyly like the KAW scheme is today. In such cases, we must fall back on practical arguments and discuss what system best serves the scientific community (e.g., Pauly *et al.*, 2009). I submit that recognition of a single genus *Anolis* achieves this goal better than recognition of a set of less familiar and mostly nonmonophyletic genera.

Acknowledgments

This work was funded by National Science Foundation grant DEB-0844624. Thanks to the members of the Poe lab (Mason Ryan, Eric Schaad, Ian Latella, Brad Truett, Julian Davis, Levi Gray, Aja King, Deidre Linden, Christine Meadows), Rich Glor, John Wiens, Kevin de Queiroz, Salvador Carranza, and an anonymous reviewer for comments and/or discussion.

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